

A NEW SUBSPECIES OF *LIMNANTHES* (LIMNANTHACEAE) FROM SAN MATEO COUNTY, CALIFORNIA

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ABSTRACT

Limnanthes douglasii R. Br. subsp. *ornduffii* E. G. Buxton (Limnanthaceae), a narrowly endemic meadowfoam from Moss Beach (Half Moon Bay) in San Mateo County, California, is described. Though it shares the morphological trait of being tetramerous with *Limnanthes macounii* Trel., an endemic species in British Columbia, Canada, it is not a sister taxon to *L. macounii* based on molecular sequence evidence. *L. douglasii* subsp. *ornduffii* appears in an unresolved group with other *L. douglasii* populations/subspecies. Molecular data coupled with morphological distinctiveness and geographical endemism provide a credible basis for recognizing the Moss Beach population as a *L. douglasii* subspecies. Data suggest that tetramerism in the genus has arisen more than once.

Key Words: Endemic, *Limnanthes douglasii*, *L. macounii*, Moss Beach, sister taxon, tetramerous.

In March 1998, I observed a large population of an unknown, tetramerous meadowfoam (*Limnanthes* sp.) while conducting fieldwork in a fallow agricultural field in Moss Beach, San Mateo Co., CA. The Moss Beach population, belonging in sect. *Limnanthes* based on petals reflexing as the fruits mature, was the first one with a tetramerous flower recorded in the USA. I contacted Dr. Robert Ornduff, University of California Berkeley (UCB), the authority on Limnanthaceae and the author of this family in *The Jepson Manual* (Ornduff 1993). After examining a specimen I sent to him, he contacted Adolf Ceska, a botanist familiar with the tetramerous *Limnanthes macounii* Trel. in British Columbia, Canada. Ceska found some morphological differences but suggested that it could be *L. macounii*, previously thought to be an endemic species of about 50 populations on Vancouver Island and a few adjacent islands in and near Victoria, British Columbia. Dr. Ornduff suggested that the *Limnanthes* population in Moss Beach could be the result of an accidental introduction from the Vancouver area (personal communication); like several of the members of the genus, including *L. douglasii* R. Br. (Kesseli and Jain 1985), this species is autogamous, therefore a single nutlet could theoretically have established the population. However, it seemed unlikely that human activity had moved the plant from Canada to California; and if dispersal had occurred via bird vectors, there should have been other known, disjunct populations between British Columbia and Moss Beach. Dr. Ornduff found it best that we co-publish a note in the “Noteworthy Collections” section of *Madroño* (Buxton and Ornduff 1998) to alert people to the possibility that the plant at Moss Beach may be *L. macounii* and that it may occur elsewhere in coastal Central California.

After growing plants from seed from the Moss Beach and British Columbia populations in a common garden, Dr. Ornduff stated “your plants are definitely not stray *L. macounii*” (personal communication). Similarly, after observing garden-grown plants, Ceska did not think that the Moss Beach plants “fit exactly anything known in British Columbia.” (personal communication). Based on the traditional morphological species concept, the plant occurring in Moss Beach would warrant recognition at species rank, perhaps even genus rank based on its tetramerism. After careful observations and measurements of the two entities grown in large numbers in the garden as well as indoors, where fruits developed in the absence of pollinators, and taking into consideration the results of a phylogenetic molecular study (Meyers et al. 2010), I am circumscribing the Moss Beach population as a subspecies of *L. douglasii*. To honor Dr. Ornduff, who called the plant at Moss Beach “a very interesting find” and asked me “to stay on it” shortly before his death (personal communication), I take pleasure in naming it *Limnanthes douglasii* subsp. *ornduffii* (Ornduff’s meadowfoam).

TAXONOMIC TREATMENT

Limnanthes douglasii R. Br. subsp. *ornduffii* E. G. Buxton, subsp. nov. (Figs. 1 and 2).—TYPE: USA, California, San Mateo Co., Moss Beach, east side of California State Route 1, opposite Half Moon Bay airport, 0.6 km S of its junction with Etheldore St., in wet portions of seasonally fallow agricultural field, elev. 18 m, 24 March 1998, E. Buxton s.n. (holotype: JEPS; isotypes: UC, CAS, DAV, UBC, DAO; paratype: R. Ornduff 10168, 12 April 1998 [JEPS 95209]).

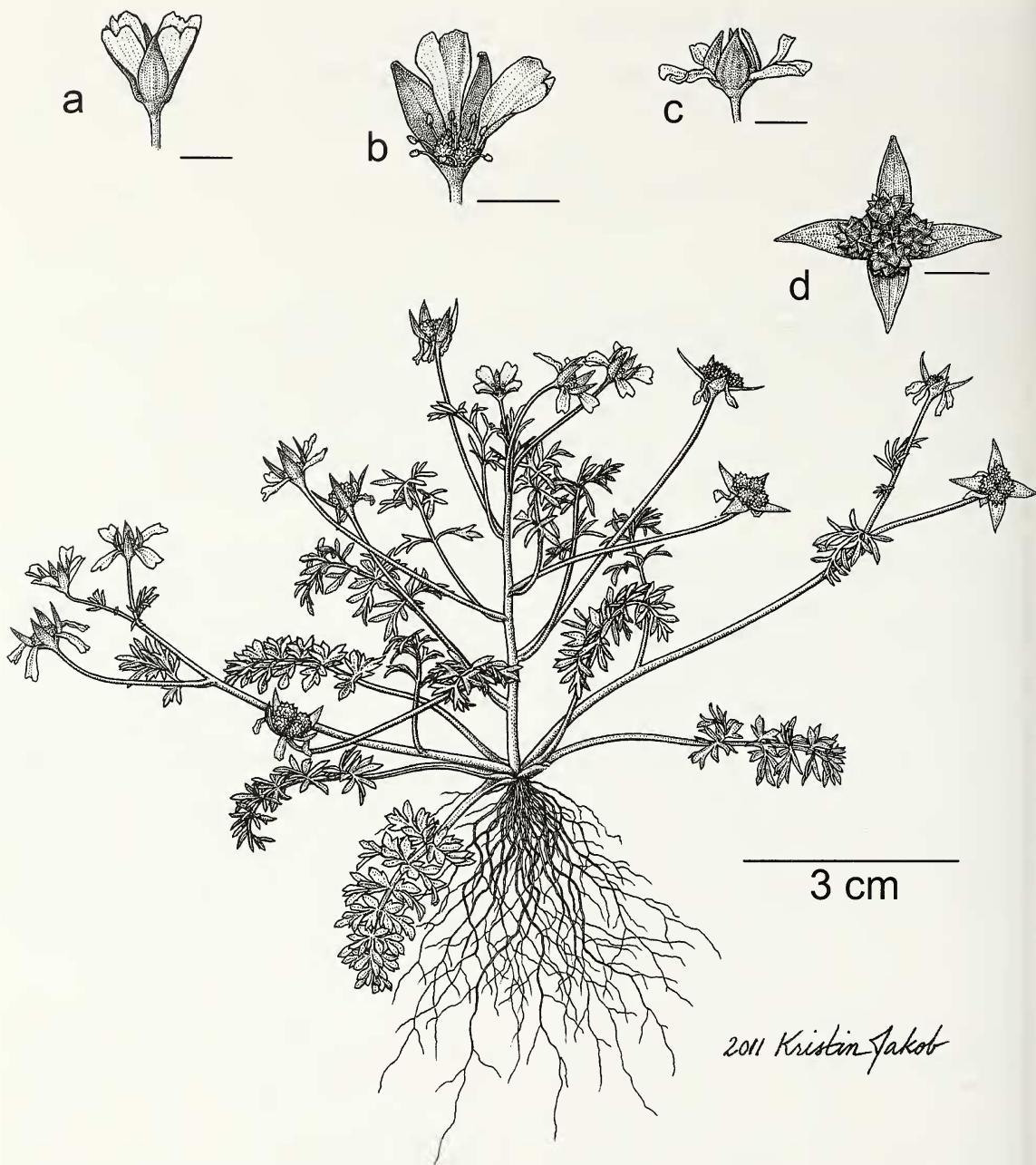


FIG. 1. *Limnanthes douglasii* subsp. *ornduffii*. a. Young flower. b. Dissected flower with stamens and style. c. Senescing flower. d. Calyx with mature nutlets. Bars for a–d are 5 mm.

Plants annual, glabrous, yellowish-green, sparingly to much branched at base. **Stems** 6–20 cm long, erect or ascending. **Cotyledons** erect. **First foliage leaves** erect, with narrowly oval distant leaflets. **Mature leaves** 3–13(16) cm long, alternate, basal leaves lanceolate to triangular, exstipulate, bipinnately divided (odd-pinnate) or incised to axis, leaflets opposite (rarely alternate) on leaf axis, petiole equaling or longer than blade; first division 3–8 pairs, 4–10(13) mm long,

second division 2–3 pairs, some lobed or toothed, 2–6 mm long; petioles of basal leaves with membranous wings, 2–3 mm wide. **Flowers** tetramerous, perfect, bowl-shaped to campanulate, at ends of bractless, axillary peduncles, peduncles somewhat compacted at distal end of stems, elongating in fruit at a ca. 90-degree angle to stem, surpassing in length axillary leaf; **sepals** lanceolate, 5–6(8) mm long, 2–3 mm wide, acuminate, elongating in fruit; **petals** cuneate,



FIG. 2. *Limnanthes douglasii* subsp. *ornduffii* in flower and fruit.



FIG. 3. Habitat of *Limnanthes douglasii* subsp. *ornduffii*.

6–7 mm long, 2.5–3 mm wide, white, faintly yellow near base, veins hyaline, tip truncate, mostly notched, erose, reflexed in fruit, claw with a few long hairs; **stamens** 8, filaments flat, ca. 2 mm long, anther ca. 0.5 mm long, yellow; **style** ca. 2 mm long, stigma 4-lobed, lobes ca. 0.5 mm long. **Nutlets** 4, ovoid, 3.5–4 mm long, 2.5–3.5 mm wide, dark reddish brown, walls strongly wrinkled, sharp-edged tubercles covering upper 3/4 of nutlet.

Phenology

Limnanthes douglasii subsp. *ornduffii* is a winter annual, germinating soon after the first rains in the fall. The blooming period lasts from (November) December until April (May). Flowering and fruiting occur simultaneously after initial growth.

Habitat

Limnanthes douglasii subsp. *ornduffii* grows in low-lying portions of an agricultural field when it is fallow (Fig. 3), as well as in drainage ditches and ruts within and adjacent to the field, in soils that are saturated to the surface for an extended period of time. In garden experiments, plants co-occurring with *L. vinculans*, a vernal pool species, survived four months of inundation. However, plants also grew to maturity in dryer conditions. The field has been planted in artichokes, fava beans, and brassicaceous plants for at least 15 yr, and is plowed at least once a year.

Distribution

Limnanthes douglasii subsp. *ornduffii* is known from a single population just south of Moss Beach, San Mateo Co. (Fig. 4). In 1998, the meadowfoam was estimated to provide a nearly complete absolute cover on ca. 18 acres; however,

its spatial distribution in the field has diminished somewhat (now ca. 90 percent), apparently due to greater competition from *Stellaria media* (L.) Vill., *Fumaria officinalis* L., *Veronica chamaedrys* L., *Lythrum hyssopifolia* L., and *Poa annua* L., and perhaps untimely plowing. In 2008, a disjunct colony of three individuals grew in a field that appeared to have been cultivated in the past, west of the Half Moon Bay airport, approximately 2.4 km from the fallow field, but this stand was not found in 2009, 2010, or 2011 (personal observation).

Table 1 presents a comparison of morphological, phenological, and ecological features of *Limnanthes douglasii* subsp. *ornduffii* and *L. macounii*. *Limnanthes d.* subsp. *ornduffii* is morphologically distinct from all other entities in the *L. douglasii* complex in the USA based on its tetramerism and much smaller flowers, and is distinct from the only other tetramerous *Limnanthes* taxon, which occurs in British Columbia. In addition to a 1400 km (860 mi) geographical disjunction, floral size, nutlet differences, and leaf



FIG. 4. Approximately 90% absolute cover of *Limnanthes douglasii* subsp. *ornduffii* on Moss Beach site.

TABLE 1. MORPHOLOGICAL, PHENOLOGICAL, ECOLOGICAL, AND DISTRIBUTIONAL DIFFERENCES BETWEEN *LIMNANTHES DOUGLASII* SUBSP. *ORNDUFFII* AND *L. MACOUNII*. Measurements and observations were made on fresh, garden-grown material of *L. d.* subsp. *ornduffii*. Data for *L. macounii* were obtained from fresh material and the Morin (2012). A. Ceska provided phenological and ecological information from British Columbia (BC).

Character	<i>Limnanthes douglasii</i> subsp. <i>ornduffii</i>	<i>Limnanthes macounii</i>
Plant	5–15(20) cm, erect or ascending; mostly branching with axillary peduncles at ca. 90° angle to stem	2–7(15) cm, decumbent (sometimes upcurved apically); mostly unbranched
Cotyledon/first leaf	erect	prostrate
Cotyledon color	yellowish green	grayish green
Cotyledon shape	oval	round
First leaf distant leaflets	narrowly oval	roundish
Mature leaf structure	bipinnate; 2° pinnae lobed or toothed	pinnate; pinnae toothed
Mature leaf length	3–13(16) cm	1–7 cm
Mature leaf, number of 1° leaflets	7–17	3–15
Sepal	5–6 mm, elongating in fruit	3–4 mm
Petal	6–7 mm	4–5 mm
Stamen/petal relationship	¼ to 1/3	½ to 2/3
Nutlet size	3.5–4 mm	3 mm
Nutlet ornamentation	sharp-edged tubercles covering top ¾ of fruit; walls strongly wrinkled	rounded tubercles, some sharp-edged on top portion; some wrinkles on walls
Nutlet color	dark reddish brown	light brown
Nutlet/sepal relationship	sepals extending beyond nutlets	sepals not extending beyond nutlets
Blooming period	(November)December–April (May) in CA.	March–early May in BC.
Start of flowering in garden-grown plants in 2004 in Marin Co., CA	January 16	February 22
Survival in sub-0°C temperature in BC.	poor to none	normal (can be imbedded in ice)
Distribution	Moss Beach, San Mateo Co., CA	Vancouver Island and vicinity, BC.

characters are distinctly dissimilar in the two taxa; the leaves in *L. d.* subsp. *ornduffii* are bipinnate to incised to the rachis, whereas those in *L. macounii* are pinnate. Foliar characters have been used in the past to distinguish species within the genus; for example, these characters “serve readily to distinguish *Limnanthes vinculans* Ornduff from all other members of the genus” (Ornduff 1969).

DISCUSSION

Molecular Analysis and Taxonomic Relationships

Plotkin (1998) conducted the first molecular phylogenetic study of Limnanthaceae using DNA sequence data, concluding that *Limnanthes striata* Jeps. may be treated as a subspecies of *L. douglasii*. *Limnanthes macounii* was also nested within the *L. douglasii* clade. Subsequently, Morin (2007) demoted *L. striata* to a subspecies of *L. douglasii*, but she left *L. macounii*, making *L. douglasii* paraphyletic. Four species and five subspecies in sect. *Limnanthes* are recognized in the Flora of North America (FNA) (Morin 2010): *Limnanthes macounii*; *L. douglasii* subsp. *douglasii*, *L. d.* subsp. *sulphurea* (C. T. Mason) C. T. Mason, *L. d.* subsp. *nivea* (C. T. Mason) C. T. Mason, *L. d.* subsp. *rosea* (Benth.) C. T. Mason,

L. d. subsp. *striata* (Jeps.) Morin; *L. bakeri* J. T. Howell; and, *L. vinculans*. *Limnanthes macounii* was maintained as a species because of its highly disjunct distribution and unique characteristics, including nutlet sculpturing and the presence of alleles at three loci found in no other taxa of the genus (Morin 2010). Ornduff and Morin (2012) include the same species as those listed in the FNA, except for *L. macounii*, which occurs only in British Columbia.

Meyers et al. (2010) conducted a phylogenetic study to resolve relationships within the genus *Limnanthes* by using one nuclear (nrITS) and two chloroplast (*trnL* intron and *trnS*-*trnG* intergenic spacer) genes. They included the meadowfoam population from Moss Beach in their survey to attempt to explain its taxonomic status and biogeographic origin. The study confirmed the monophyly of two sections within *Limnanthes*: *Limnanthes* (= *Reflexae*) and *Inflexae*. They concluded that the results of the molecular study, as well as crossing experiments, did not support taxonomic recognition of the Moss Beach (Half Moon Bay) population, rather it is “part of a highly polymorphic *Limnanthes douglasii sensu lato*” and is an ecologically interesting and morphologically divergent population within this polymorphic species. They further suggest that the divergence of extant taxa may have been a

recent and rapid event and too few mutations have accumulated in the genes or were detected in the markers tested. This supports the notion that non-resolution in cladograms is not uncommon with closely related taxa, i.e., purported subspecies.

Locating Populations

Repeated attempts to locate additional populations of a tetramerous meadowfoam along the coasts of Washington, Oregon, and California have failed. Ceska (Ceska and Ceska 1999) suggested that the present range of *Limnanthes macounii* in British Columbia is a northern extension of an originally more southerly distribution of this species, which together with various other southern floristic species spread during the Hypsithermal period; *L. macounii* either became extinct or has been overlooked. Consequently, at his suggestion, concentrated efforts to locate this species in California were made in 1977 by Ph.D. students at UCB and UC Davis (UCD). No populations were found, and they concluded that this species could not have been overlooked, if, in fact, it grew in California (Ceska and Ceska 1999). I have searched wet portions of the hills to the east of the agricultural field, wetlands south of Montara and to the north of the site, and some areas between Moss Beach and Santa Cruz, but have found only the small stand on the west side of the Half Moon Bay airport in 2008. Meyers et al. (2010) unsuccessfully attempted to locate tetramerous plants in California and Oregon during four field seasons. No such meadowfoam populations were found during thorough field surveys between Devil's Slide and Pescadero (San Mateo Co.), including agricultural fields and marshes on the east side of State Route 1, conducted in preparation for *Plants and Plant Communities of the San Mateo Coast* published by San Mateo Coast Natural History Association in 2009. Dr. Dean W. Taylor (independent botanist) has done floristic surveys in Santa Cruz and San Mateo counties, and has searched agricultural settings along the coast from Santa Cruz toward Moss Beach without finding any meadowfoam populations (personal communication). The closest documented *L. douglasii* subsp. *douglasii* populations historically occurred ca. 10 km to the east (San Andreas Lake, San Mateo Co.) and ca. 55 km to the north of Moss Beach (San Rafael, Marin Co.) (CCH 2010). *Limnanthes d.* subsp. *sulphurea* (JEPS 19572) grows in a marshy area near the town of Pescadero, 40 km to the south (N. Kramer, Kramer Botanical, personal communication).

Human History of Site

The natural environment in parts of the San Mateo coast has experienced great transformation

over the past centuries and many native plant communities were likely changed or eradicated in the early to mid-1800's. In 2010, a historic research study document was prepared in connection with the acquisition of the *Rancho Corral de Tierra* (*Rancho*), which included the agricultural field now supporting the meadowfoam, by the Golden Gate National Recreation Area (GGNRA) (NPS 2010). The field is presently owned by the Peninsula Open Space Trust (POST) and leased to Cabrillo Farms. The document traces the human history of the *Rancho* area, revealing how land usage has changed from the Ohlone Indians burning the landscape for centuries to improve grazing for large game, to the raising of cattle and sheep by the Mission fathers in the late 1700's. In the 1800's, the land was mainly used for dairy farming and production of hay, grains, and potatoes. In April of 1860, the *San Mateo Gazette* declared the *Rancho* as "one of the most productive ranchos of its kind mainly for grain and stock grazing in California" (NPS 2010). This gave way to a floriculture and modern agriculture growing vegetables, including Brussels sprouts and artichokes in the late 1900's and early 2000's. The Half Moon Bay Airport, located directly west of the field, was constructed in 1942 for the U.S. Army.

CONCLUSIONS

I propose that *Limnanthes douglasii* subsp. *ornduffii* is a relic taxon that arose independently and is persisting in wet depressions, fed by seeps and small streams still in existence in the hills directly east of the agricultural field. In the past, the Moss Beach area was likely a marine terrace/coastal prairie with various types of wetlands forming during the wet season. The taxon may have been more widespread before its habitat was altered or destroyed by cattle grazing, agriculture, and urban development during past centuries; thus, extirpated populations could have flourished in areas of similar soils and hydrology. Non-native species have invaded many plant communities in California, including wetlands, where they have outcompeted native species. The Moss Beach taxon is likely persisting in the agricultural field due to the continual disturbance and removal of competing plants during the plowing of the field every year. This view has also been put forth by Plotkin (unpublished), who stated in regards to the Moss Beach taxon that "it is certainly not impossible that it is a remnant population that persists here."

Limnanthes douglasii subsp. *ornduffii* is morphologically distinct from all other sect. *Limnanthes* taxa based on its tetramerism and smaller flowers and is also distinct from *L. macounii*, the only other tetramerous taxon. *Limnanthes douglasii* subsp. *ornduffii* groups with some *L.*

douglasii populations/subspecies and not with *L. macounii* in Meyers' et al. (2010) cladogram. This clustering suggests that tetramerism has evolved more than once in the genus, thus tetramerous floral morphology is homoplastic within *Limnanthes*. The Moss Beach taxon is described at the rank of subspecies on the basis of its alignment with *L. douglasii* in the cladogram. Until additional data on the taxonomic, evolutionary, and biogeographic relationships of the Moss Beach plants are obtained that present greater resolution within sect. *Limnanthes*, this population warrants taxonomic recognition at the subspecific level.

Conservation Consequences

Not recognizing the various morphological entities, including *Limnanthes douglasii* subsp. *ornduffii*, would be a deterrent to the legal protection of disjunct, rare populations in the *L. d.* complex. Meyers et al. (2010) suggest that it might be a benefit to conservation work to merge the various *L. douglasii* taxa, as that would result in a greater amount of genetic diversity available for restoration. That would, however, result in no protection for rare taxa within the *L. douglasii* group. For example, it would be possible to mitigate for *L. d.* subsp. *sulphurea* (state-listed as endangered and occurring in a few colonies on the Point Reyes peninsula in Marin Co. and near Pescadero in San Mateo Co.), and *L. vinculans* (federally- and state-listed as endangered and endemic to a few vernal pools in Sonoma Co.), by using *L. d.* subsp. *douglasii*, a very common wetland plant throughout most of California. (The California Environmental Quality Act [CEQA] mandates mitigation for impacts to listed and other rare or endangered species.) By considering *L. douglasii* a polymorphic species, protection of morphological distinctiveness and geographical endemism would be lost.

Based on NatureServe criteria (Faber-Langendoen et al. 2012), *L. douglasii* subsp. *ornduffii* is eligible for a G1 designation, indicating that the taxon is *critically imperiled* across its entire range due to only one known occurrence. Based on IUCN (2010) criteria, the taxon may qualify for Red List Category *Vulnerable*—high risk of endangerment in the wild—because of its only known occurrence in an agricultural field. However, as repeated disturbance of the habitat of *L. douglasii* subsp. *ornduffii* appears to be the reason for the plants' persistence in the agricultural field, no protective measures relating to this subspecies and its habitat should be necessary. Seeds should be collected and deposited in a botanic institution that is a participating member in the Center for Plant Conservation's network to serve as a resource in reintroduction projects should a

devastating event eradicate the only known occurrence.

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